NOTES AND LITERATURE

HEREDITY

A Case of Non-Mendelian Heredity.—That hereditary characters which behave in accordance with Mendel's law of segregation depend in some way upon the chromosomes can hardly be questioned. Biologists, however, have been loath to believe that all hereditary characters are thus related to chromosomes. It is especially gratifying, therefore, to find completely worked out a type of inheritance which differs radically from the Mendelian type and which appears to be entirely cytoplasmic in character. The law of transmission in this case is of unusual interest. The case is reported by Dr. Erwin Baur, of Berlin.[1]

In this paper Dr. Baur describes several types of variegation. The first consists of variegation due to pathological conditions (auto-infection or auto-intoxication) and is not hereditary. By overcoming the auto-intoxication such plants are converted into ordinary green plants. On the other hand, ordinary plants can be infected with this condition by graft-symbiosis with an infected plant. This condition is not transmitted by seed. It is called by the author "infectious chlorosis," and is accompanied by a partial loss of green pigment in the chlorophyll grains. Several previous papers on this type of chlorosis by the author are referred to.

The second type of variegation consists of fully constant races whose chromatophores carry a diminished amount of green coloring matter, but the normal amount of yellow coloring matter. These races have distinctly yellowish-green leaves. In crosses with green races the yellowish green behaves as a Mendelian recessive.

The readers of this journal will remember that a similar character in tomatoes was reported recently by Professors Price and Drinkard, of the Virginia Experiment Station, and the character in this case behaved also as a Mendelian recessive.

[1] Erwin Baur. The Nature and Hereditary Relations of the Albo-Marginate Horticultural Variety of *Pelargonium zonale*. *Zeitsch. f. Abst.- u. Vererb.*, Bd. I, 1909, H. 4.

In another class of yellowish-green races, which are in a sense constant, the yellow-green plants are all heterozygote and Mendelize into one fourth clear yellow incapable of development, one fourth pure green, constant in later generations, and two fourths yellow-green, which splits again as above. This case was treated of by Dr. Baur in a former paper.[2]

Many other types of variegation exist. One of them is reported in the review of Professor Correns's paper below. The present paper of Dr. Baur's deals with another type of variegation, namely: white margined leaves, such as those found in varieties of *Acer negundo, Cornus alba, Pelargonium zonale* and numerous other species. The investigation was confined largely to the last-mentioned species. Little was previously known of the inheritance of this character. Several authorities had stated that such plants (with white margined leaves) produce only seedlings that are pure white and incapable of development.

Dr. Baur's studies show that the white margined plants of *P. zonale* are covered with two or three layers of cells containing colorless chromatophores which can not assimilate CO_2 but which can manufacture starch from sugar. The whole plant is covered by this white tissue. Near the leaf margin the two white layers form the whole of the tissue and thus give the peculiar marking on these leaves.

The line of demarcation between the white cells and ordinary cells is definite. One gets the impression that all the descendants of a white cell are white and all those of a green cell are green. This can not be definitely determined by microscopic study, but the experimental results reported below practically prove that such is the case.

Four white margined plants obtained from different sources all, when self-fertilized, produced only white seedlings, which soon died because they were incapable of assimilating CO_2. Some of these plants occasionally produced green branches which arose by the green tissue breaking through the superficial covering of white. Seed from these green branches produced normal green plants which propagated true to seed. On the other hand, white branches, when close fertilized, produced only white seedlings. (An occasional branch was pure white without the underlying green tissue.)

[2] *Ber. d. Deu. Bot. Gesell.*, 25, 1907, p. 442, and *Zeitsch. f. Abst.- u. Ver.*, 1, 1908, p. 124.

Crosses made between flowers on pure white branches and other flowers on ordinary green plants gave thirty-nine green seedlings and seven green-white marbled plants. These crosses were made both ways, but only one seed, resulting in a green plant, was raised from the cross of green (♂) on white (♀).

Several crosses made both ways between white margined plants and ordinary green plants gave 199 pure green, 41 green-white marbled, and 4 pure white seedlings. Crosses between white margined and pure white branches gave all pure white seedlings. Evidently, white branches and white margined branches produce only white gametes, while green branches or green plants produce only green gametes.

Of the green-white marbled seedlings—that is, green and white spotted, some formed only white leaves and died when the spotted cotyledons ceased to function.

A second class formed only green leaves and became ordinary green plants when the spotted cotyledons dropped off. Their seedlings, about 50 in number, were all ordinary green plants.

A third class grew stems that were white on some sides and green on others. On such stems leaves attached to white surface were wholly white, and those attached to green surface were wholly green. Leaves attached on the line of union between green and white were correspondingly green and white. Branches which grew from the axils of the leaves behaved in exactly the same way as the leaves in regard to the green and white color.

These facts render it clear that the marbled seedling consists of two kinds of tissue—green and white. The descendants of white cells are white and those of green cells are green. A green and white seedling or branch may become either green or white by the growing point becoming overcapped by the one or the other kind of tissue. Of 23 marbled plants observed 20 became green and two white in this manner.

But the development of a marbled branch or plant may proceed in a different manner and one which clears up the difficulty concerning the nature and hereditary relations of the white marbled plants. In a marbled stem the line of contact between the two kinds of tissue may extend radially inward, or the white tissue may extend in a thin layer some distance over the green. A leaf rising centrally on a line of contact extending radially inward will be half white and half green; but a bud originating

from a part of the stem where the green tissue is covered by a thin layer of white is itself constituted of green tissue covered by white and produces ordinary white margined leaves. New albomarginate plants may thus be obtained from these marbled seedlings by taking branches which thus arise from parts of the stem where the white tissue forms a thin layer over the green. The white margined plants are thus to be regarded as "periclinal chimeras," while the marbled plants are "sectorial chimeras." White or green branches may arise from the white margined plants as the result of irregularity in cell division at the growing point.

The inheritance of the albomarginate character is now clear. In a white margined plant pollen and ovules are produced from white tissue only and hence carry only the white character. The seedlings are therefore white.

Sectorial chimeras were found in which the green tissue was superficial and the white central, thus giving leaves that were green on the margin and a paler color in the center, on account of the white tissue in the center of the leaf. One of the plants grown from a green branch occurring on an albomarginate plant was of this nature. Its seed produced only ordinary green plants.

The origin of the mosaic seedlings from a cross between white margined and green is not yet fully clear. Careful study of such of these seedlings as were recorded pure white revealed indications of green tissue in the hypocotyls. Likewise, those regarded as pure green revealed indications of white tissue. All of the seedlings from the green-white cross are probably mosaics, the differences being due to the fact that in some of them the white tissue, in others the green, is confined to a few cells, the remainder of the plant developing from the other tissue.

It is important to note that in some of these mosaics, or marbled plants, white "islands" may appear in several parts of the plant. These islands are evidently not derived one from the other. It can, therefore, be asserted that the differentiation of these white cells occurs more than once during the development of a plant and that the white cells must result from the division of cells that are green in appearance. (It is important to remember that green is dominant in the cross.) Just when these white cells arise can not be stated so positively. They may certainly arise after the formation of the cotyledons has begun.

The author offers the following tentative explanation of the origin of this white tissue in the crossbred green-white plants. The fertilized ovum contains both green and white chromatophores. In cell divisions of the embryo the chromatophores are distributed to the daughter cells more or less according to chance. If a cell receives only white chromatophores this cell will have only white descendants. If a cell receives only green chromatophores its descendants will be pure green cells. A cell receiving both kinds may later produce either pure white or pure green at any cell division. Should a cell which is later to develop into cotyledons and growing point receive only one kind of chromatophores, then the resulting seedling will appear to be only pure white or pure green, as the case may be. Since pure white cells may have only pure white descendants and pure green only pure green, while mixed cells may have three kinds of descendants, it naturally follows that after many cell divisions the percentage of mixed cells in the plant practically vanishes.

The above hypothesis makes only one assumption that is not demonstrated; that is, that the fertilized egg cell has two kinds of chromatophores, namely: white and green. According to current teaching the chromatophores are derived entirely from the egg cell; but, according to the author, this may well be considered not an established fact. If current teaching on this point is correct, then we have here a very remarkable case. It would then be necessary, according to Dr. Baur, to assume that in the cross, female white on male green, a part of the white chromatophores of the egg may become green under the influence of the male nucleus, and that in the reciprocal cross a part of the white chromatophores would have to become green under the influence of the male nucleus. Such a condition is thinkable, but no such case is known. Should it be proven, however, that the male sexual cell carries chromatophores, then the inheritance of the albomarginate character is fully explained.

These results of Dr. Baur's call for a detailed study of the chromatophores from one sexual cell stage to the next. The writer would suggest another possible explanation of the phenomena discussed above. The male nucleus may bring with it into the cell something which is not a part of the nucleus itself but is cytoplasmic in its nature. This may develop and give rise to a part of the cytoplasm of the fertilized egg. Then something in the chemical constitution of this cytoplasm causes the chro-

matophores which develop in it to lose their power of assimilating CO_2. Subsequent cell division would occasionally throw off cells of pure white, which would give rise to the white tissue. This is only suggested as a mere possibility. That the condition can hardly be caused by the male nucleus itself would seem to be indicated by the fact that descendants of this nucleus must be present in those cells which are pure green. If the white character were carried by the chromosomes, then it would appear that all the green cells would necessarily be affected. There seems to be no question that the white character is cytoplasmic in its nature, and this would account for the fact that it does not follow Mendel's law of segregation in the reduction division. The segregation, in fact, occurs in somatic divisions.

Professor Correns reports another interesting study of variegation in a recent article,[3] of which the following is a summary.

Plants deficient in chlorophyll have hitherto been called "aureas." The author now restricts this term to plants which are deficient in chlorophyll but which have the normal amount of yellow-color materials, zanthophyll and carotin. Those deficient in all three are termed "chlorinas." Those of the latter type obtained in commerce were found to be dwarf as compared with normal sorts. The leaves and flowers are also relatively smaller. This smaller size is shown to be partly a consequence of deficiency in chlorophyll and the consequent insufficient nourishment of the plant. On the other hand, it is partly due to a specific Mendelian character of dwarfness, and the Mendelian dwarf habit is strictly correlated with small leaves and small flowers.

The chlorina races are fully constant. Variegated races have spots of green on leaves otherwise of chlorina type. In some cases these spots vary in number and size from leaf to leaf; in others they are hereditarily fixed. Some of the variegated races, on account of the smallness of the green spots, are difficult to distinguish from the chlorina types. On some of the variegated plants, especially those having much green, typical green branches occur, and this phenomenon is characteristic of the plants on which it occurs. That is, the same plant year after year produces these green branches. Every possible gradation

[3] Investigations on Inheritance of Yellowish Green and Variegated Races of *Mirabilis Jalapa*, *Urtica pilulifera* and *Lunaria annua*. *Zeitsch. f. Abst.- u. Vererb.*, 1, 1909, H. 4.

exists between a small green fleck on a leaf and a typical green branch.

The variegated types do not reproduce strictly true to seed. They sometimes throw green plants. These green plants do not simply represent extremes of variation because they are too numerous and offer a secondary maximum in the curve of distribution. On the other hand, variegated plants have thus far not produced any of the pure chlorina type. Some of the pure green reversions produced progeny all of which are green. A larger number gave some variegated and some green, the green nearly always predominating in the progeny. The thus obtained variegated plants gave some normal green progeny, and the normal greens thus obtained gave only occasionally all normal greens. A green branch on a variegated plant, when self fertilized, gave three variegated and four green plants. It was not possible to explain variegation in these species as a cross between the chlorina and the normal green types. In the cross between chlorina and typica (normal greens) the latter is dominant, but not absolutely so. The chlorophyll content of the hybrids is about 90 per cent. of that in the normal greens. In some cases in the second generation of this cross, the hybrids split into chlorinas and greens in perfect Mendelian fashion. In others variegated plants occur in the second generation; the reason for this is given below.

Dwarf and normal stature behave as a pair of Mendelian characters independent of leaf color, the dwarf habit being recessive. Generally speaking, chlorina plants not dwarf were not quite so tall as the normal greens because of their inability to manufacture starch at normal rate. The tall chlorinas and the dwarf greens produced from this cross were new types, the latter being especially attractive.

In the cross variegata on typica the latter is dominant and segregation occurred in Mendelian fashion. On account of the variability of the variegated type (this type produced some greens) the per cent. of greens in F_2 was somewhat in excess of 75 per cent. Here again the semi-dwarf and normal stature acted as a pair. In the cross between chlorina and variegata the latter proved to be dominant. Normal splitting occurred in the second generation. As in other cases, a few greens arose from the variegated plants. The medium stature of the variegated plants behaved as a pair with the dwarf stature of the chlorina plants.

In each of three experiments the cross variegata on typica gave chlorinas, variegated plants and normal greens in the ratio 1 : 3 : 12. The plants used in these crosses were known to be constant. In one experiment a cross between typica and chlorina gave in F_2 63 green, 4 variegated and 3 chlorinas. Here also the chlorina form was known to be constant. This unusual behavior is explained by Professor Correns in the following manner:

The occurrence of normal greens amongst the progeny of variegata is due to the revival of a latent factor for green (G). The color factors present in the various types are assumed to be

G = presence; g = absence (or latency) of green factor.
V = presence; v = absence (or latency) of variegata factor.
C = presence; c = absence (or latency) of chlorina factor.
V is epistatic to C.
G is epistatic to V and C.
Variegated races have the formula gVC (or gVc).
Chlorina races have the formula gvC.
Normal green races have the formula GVC (or GvC, or GVc, or Gvc).

The cross between green and variegata thus becomes:

GVC + gVC, in which F_2 = 3 green to 1 variegated; or
GvC + gvC, in which F_2 = 12 green, 3 V and 1 C.

The cross green on chlorina becomes:

GvC + gvC, in which F_2 = 3 green to 1 chlorina; or
GVC + gvC, in which F_2 = 12 green, 3 V and 1 C.

The cross variegated on chlorina becomes:

gVC + gvC, in which F_2 = 3 V + 1 C.

The cross between the very distinct species *Mirabilis Jalapa variegata* and *M. longifolia* typica give hybrids that are quite alike in F_1, but highly variable in F_2. Yet all the characters involved appear to "Mendelize." For instance: green and variegated leaves, normal and dwarf stature, erect and trailing habit form Mendelian characters.

In contradistinction to the white margined *P. zonale* studied by Baur, a white margined form of *Lunaria annua* studied by Professor Correns reproduced true to seed, and when crossed with a green leafed form the margin behaved as a recessive Mendelian character.

A recent article by Whitney in the *Journal of Experimental Zoology*[4] is of interest in connection with the type of heredity

found by Baur in *P. zonale*, as it bears upon the relation of plastids in the cytoplasm to heredity. Eggs of *Hydatina senta* were subjected to centrifugal force, which separated the contents into three layers, described as a pink zone, a middle clear zone and a gray zone. The first cleavage plane was variously arranged with reference to these zones in different eggs, yet the eggs developed into normal adults which produced normal young. This would seem to indicate that the plastids in the pink and the gray zones have little to do with differentiation in development. This does not prove, however, that other plastids might not have such influence.

Professor Vernon L. Kellogg, of Leland Stanford University, has recently published an important paper on inheritance in silk worms.[5] In common with Coutagne and Toyama he found many Mendelian characters in these insects. This was especially the case for characters of the larvæ. For instance, the mouricaud pattern (a dark form) in the larvæ was dominant to white. The same was true of the tiger banded, or zebra, type of coloring. A white type with a well marked darker pattern, which in the laboratory is known as "the patterned type" behaved usually as a unit character recessive to zebra and dominant to white. Its behavior was entirely Mendelian in crosses with white, but there was some irregularity in crosses with zebra. The irregularities mentioned by Professor Kellogg are fully explained by assuming that the pattern character and the zebra character are independent Mendelian characters, and that when both are present in the same individual they can both be discerned.

The author was puzzled a good deal by the behavior of white and attributes the fact that it was sometimes dominant and sometimes recessive to individual or strain idiosyncrasies. A large number of matings are given with their results in the first and second generation to illustrate the idiosyncrasies relating to inheritance of white. Evidently, Professor Kellogg was dealing with animals in which there are two distinct types of white, one dominant and the other recessive. A similar case has been well made out for poultry, and I have found indications of two such white characters in swine, though the recessive white in swine is not fully made out. All of the irregularities in the inheritance

[4] D. D. Whitney. Effect of a Centrifugal Force upon Development and Sex. *Journ. of Exp. Zool.*, VI, No. 1, January, 1909.

[5] Leland Stanford University Publications, University Series No. 1.

of white found by Professor Kellogg fall immediately into line with Mendelian principles by the assumption of these two types of white, which are sometimes found in the same individual.

Some of the most interesting work reported by Kellogg relates to cocoon coloring. He found one type of salmon colored cocoon which when crossed with either the dominant or the recessive white behaved as a Mendelian unit and broke up into every shade from very pale salmon to golden yellow. This is an interesting case of a variable Mendelian character. Generally speaking, the various cocoon colors were Mendelian units, the only irregularity being the marked variation of some of the colors after hybridization. Wing pattern in the adults and the color and adhesiveness of the eggs showed no Mendelian differences. Apparently the variations which occur in these characters are due to the fluctuations of a single Mendelian character, and hence no pairs are formed.

The effect of insufficient nutrition on the dominance of characters was studied, the results being entirely negative. Kellogg attributes the Mendelian nature of the larval color characters to their origin by mutation, while the fluctuating variability of cocoon characters are supposed to be due to their origin by selection of fluctuating characters. As pointed out by the writer elsewhere, the manner of origin of a character, whether by gradual modification or by sudden change, has no relation to its Mendelian behavior, so that the fact that certain characters behave as Mendelian characters is in no way an indication that they are mutations.

Certain characters which fluctuated widely, and in which no indication of Mendelian inheritance was found, were amount and quality of silk in the cocoon, wing pattern, wing venation, certain larval markings, degree of adhesiveness in eggs and the number of broods produced in a season. These characters present very interesting objects of study, and it is gratifying to learn that Professor Kellogg is giving them further attention. Coutagne is quoted to the effect that selection for ten years had no effect on the richness of silk. This is important in its relation to the effect of selection on fluctuating characters.

One of the races on which these studies were made lays eggs which are non-adhesive. When crossed with races laying adhesive eggs, the non-adhesiveness disappears and does not reappear even in the second generation ordinarily. This suggests

that non-adhesiveness is due to the latency of a character which is revived under the stimulus of hybridization. It is stated that wing pattern does not seem to be capable of any considerable modification by even a most careful and persistent selection. This is in line with all recent work on selection in fluctuating characters when the effect of hybridization has been eliminated.

Variations of wing venation are of special interest. They seldom took the form of additions to the system of veins, and when they did the modifications were only slight. Generally, these variations consisted of the loss of veins in part or in whole. In many cases veins became reduced to tracheæ without chitinous covering. In a few cases tracheæ appeared in what may be supposed to be the position of ancient veins, thus representing partial restorations of lost characters. Many sports occurred in wing pattern. Generally speaking, these were not hereditary. Melanism occurring as a sport showed a slight tendency to be inherited, and further studies of this matter are in progress. Occasional moths with power of flight and less frequently appearing individuals with rudimentary wings showed no tendency to transmit these characters.

Some of the most interesting features of Professor Kellogg's work are the marked fluctuations of characters whose stages can not be fixed by selection. Yet the fact that certain of the races were constant with respect to a particular stage of such a character, as, for instance, the Italian salmon with reference to cocoon color, which on hybridization breaks up and becomes highly fluctuating, is of great interest. The question whether fluctuations can be fixed by selections is as yet debatable. The Italian salmon seems to be such a fixed stage. On the other hand, some of Professor Kellogg's results indicate that the Italian salmon may be a compound character, a fact which might account for its variability. Perhaps long continued selection might, after a while, fix such characters, especially when the fluctuations cover such a wide range. The writer hardly agrees with the assumption that such characters are non-Mendelian. It would seem rather that their stages are simply not stable from generation to generation. If they could be fixed by selection or otherwise one might then expect the fixed stages to behave toward each other as Mendelian pairs.

Dr. East reports some interesting studies on inheritance in

sweet corn.[6] He points out that Correns has shown that the peculiarity of sweet corn is due simply to inability to complete the formation of normal maize starch. The presence and absence of this starch forming ability behaves as an ordinary Mendelian pair. The absence of the ability to form starch is the one character peculiar to the sweet corn group. It is shown that the sweet corn may be either of the dent or the flint type in potential hereditary characters, and suggests that the early history of sweet corn indicates that it arose amongst the flints and spread to the dents by hybridization. Dent corns tend to have from 12 to 28 rows; flints usually have 8 and may have 12 rows as the mode. Dents are little given to tillering, while tillering is characteristic of flints. Flint varieties are also characterized by large bracts at the end of the husks, dents by small bracts or none. Sweet corn, on the other hand, runs the whole gamut of the above characters. For instance, Stowell's Evergreen is a dent, having 16 to 24 rows. Golden Bantam and Black Mexican are flints.

When the starch forming character is introduced into sweet varieties from either dent or flint sources the dent or flint character of the sweet parent becomes evident. The author thinks that the dent or flint character appearing in sweet corn is determined largely, but possibly not entirely, by the character possessed by the female parent.

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[6] E. M. East. A Note Concerning Inheritance of Sweet Corn. *Science*, N. S., XXIX, No. 742.